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REPRODUCTION IN PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 195

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In connection with the vast accumulation of facts concerning reproduction, our morphological categories are in danger of becoming too rigid. Emphasis is laid upon secondary features, and the fundamental features common to all reproduction escape attention. An extensive terminology further enforces rigidity of classification, because terminology makes exact definitions necessary. As a consequence, the various so-called "types" of asexual and sexual reproduction are pigeon-holed in our texts as though they had nothing in common. It is the purpose of the present paper to attempt a tentative analysis of the phenomena of reproduction as observed in plants, to eliminate the secondary features that make for too great rigidity of conception, and to discover the facts which are common to all reproduction, which underlie all superficial differences, and which, therefore, relate naturally the various "types." It is hoped that such an analysis may serve, not only to soften morphological distinctions, but also to suggest research that will deal with fundamentals more than with superficial details. In such a presentation it would be impossible and confusing to pay attention to all of the variations recorded. Only the general situations can be included, so that the conclusions reached will not seem to satisfy every case, but the point of view will be indicated which can eventually adjust all details.

The use of the term "reproduction" in this paper must be defined. Any cell that produces another one is performing the function of reproduction, but the result may be merely the growth of an individual, the restoration of wasted tissue, or the healing of a wound. Reproduction will be used as meaning the production of new and independent individuals, which is the current understanding of the word.

Vegetative multiplication

In one-celled plants the individual and the cell are identical. Among the varied activities of the protoplast, the power of self-division is one, and in such plants this division results in two new individuals. In other words, this is reproduction, and the conclusion is that the fundamental mechanism of reproduction is cell-division. There is nothing more in the machinery of reproduction than this phenomenon of cell-division, whether it be sexual or asexual reproduction. If the essential machinery of reproduction is provided for in cell-division, it follows that the cell-fusion connected with the sex act must be regarded as an addition to the fundamental process of reproduction, an added preliminary process, not necessary to reproduction, but securing something in connection with it. In fact, the extent to which asexual reproduction occurs among plants is not fully appreciated. It is probably true, taking the plant kingdom as a whole, that the multiplication of individuals is greater by asexual than by sexual methods. The abundant asexual reproduction even among angiosperms testifies to the fact that asexual reproduction is not even a declining method. What may be called the first stage in the evolution of asexual reproduction, therefore, is represented by those one-celled plants whose only method is ordinary cell-division, which is a function exercised by any protoplast under appropriate conditions.

Reproduction by spores

Among many-celled plants, ordinary cell-division usually does not result in new individuals, but in the growth of the individual. This transition from cell-division resulting in new individuals to cell-division resulting in growth is associated with the establishment of a new form of asexual reproduction. So long as protoplasts are held together by their walls in the continuous framework of an individual, there can be no production of new individuals. There must be detachment from the parent stock as a preliminary to the series of cell-divisions that are to result in the new individual. Among the lower algae this is accomplished in a very simple way. The protoplast detaches itself from the cell wall and

escapes into the surrounding medium. The escaped protoplast (spore) is nothing more than a protoplast acting independently of its wall and of its parent plant. No new powers seem to belong to the escaped protoplast; it begins a series of divisions, but being free from the parent form, the divisions result in a new individual. The difference between such a spore, therefore, and any other protoplast belonging to the parent body is not a difference of power but of opportunity.

Ordinarily the spore-forming protoplast begins a series of divisions before escape, resulting in several spores; but it is obvious that the series of cell divisions is responsible for reproduction, whether the protoplast divides before it escapes, or escapes before it divides. In many fungi the detachment of spores is secured, not by the discharge of protoplasts, but by the abstriction of walled cells from special branches. This "pinching off" a part of the body is merely a detail of separation. The essential fact is that a spore means a protoplast separated from one individual, and capable of producing another individual. The multitude of names applied to spores on the basis of secondary characters has obscured the fundamental idea that belongs to all of them, the idea of a detached protoplast.

It would be interesting to know what conditions determine the separation of a protoplast from its wall and its abandonment of the structure it has made and kept in condition. A possible suggestion may be obtained from the occasional behavior of protoplasts at the inception of conditions unfavorable to vegetative activity. Just as in spore-formation, the protoplasts become freed from the wall, round off, and are entirely detached from the general life of the individual which has produced them. The experimental control of spore-formation in many algae and fungi shows that conditions can be supplied which inhibit spore-formation indefinitely, and other conditions can be supplied which stimulate abundant spore-formation. In general, whatever diminishes vegetative activity favors spore-formation, so that it is the physiological condition of the protoplast that determines whether it continues to do vegetative work, or becomes a spore. It is certainly suggested that the favorable condition for spore-formation in nature

is the waning activity of the protoplast. The conclusion is that spore-formation is a response to relatively unfavorable conditions on the part of plants whose activity extends through a period long enough to encounter varying conditions. This would make spore-formation possible among one-celled plants, as well as among many-celled plants.

One of the problems of reproduction, perhaps to be regarded as the most fundamental one, has been suggested by the previous statements. When protoplasts are detached from a parent plant, whether it be a single protoplast called a spore, or a group of protoplasts, as in the case of a propagating bud, the whole structure of the parent is reproduced. Of course the essential separation is physiological, which may take place although complete structural separation has not been effected. When one considers the reproductive power in a group of active cells isolated from the parent stock, such as gemmae, propagating branches, buds, tubers, bulbs, cuttings, isolated nodes, and even leaf fragments, it becomes evident that reproduction is a function of every active cell, and that it can express itself when certain conditions are supplied. The conspicuous condition seems to be detachment from the parent stock. It is really a restoration of lost parts, and therefore is a form of regeneration, differing in degree but not in kind from what is ordinarily called regeneration. From this point of view, a spore is to be regarded not so much as a specialized reproductive cell, differing in power from other protoplasts, but as a single detached protoplast rather than a group of them, and therefore regenerating all the structures of the body. What induces these detached protoplasts, whether single or in groups, to produce a new individual is no more clear than what induces a fertilized egg to produce a similar structure, but both seem to belong to the same category, and that is, a series of divisions that result in a definite structure.

A further stage in the evolution of spore-formation is the differentiation of sporangia, which needs no discussion in this connection. Sporangia are formed under the conditions that favor spore-formation, and not during maximum vegetative activity. They are not formed as parts of the body, awaiting appropriate conditions for spore-formation. The fundamental difference

between plants without and with distinct sporangia is that in the former all protoplasts may respond to the conditions for spore-formation, while in the latter only a restricted number of protoplasts respond. What determines the selection is a question that remains for physiology to answer. When the differentiation of sporangia first takes place, the vegetative cells have either lost the power of spore-formation once common to all vegetative cells, or are inhibited from expressing it. Spore-formation by cells ordinarily vegetative occurs often enough to assure us that spore-formation is only inhibited in such vegetative cells.

A summary of what may be called three stages in the history of asexual reproduction, as given above, may be stated as follows. The first stage is represented by cell-division, which belongs to cell-activity in general; in other words, it is a process as natural to all protoplasts as any work. The second stage is represented by spore-formation, in which ordinary vegetative cells under certain conditions produce spores. In this case the activities of a cell are differentiated by varying conditions, and are not differentiated permanently. The third stage is represented by the reproduction of spores by special cells which are differentiated in function permanently from the ordinary vegetative cells. This specialization of certain cells is accompanied by the inhibition of the spore-producing power of cells in general.

The origin of sex

If all plants were sexual, the origin of sex would be as obscure a problem as is the origin of life. Fortunately for this problem, the most primitive plants are sexless, and the gametes are seen to be as definitely related to previous structures as are any other features of evolutionary progress. What is ordinarily referred to as the "origin of sex," however, is simply the morphological origin of gametes, the visible structures associated with sex. The use made of *Ulothrix* as an illustration in this connection is familiar to all botanists. The gradations from zoospores to gametes are complete, so that it seems to be clear that in this case gametes are morphologically spores greatly reduced in size, and usually incapable of functioning as spores. It is a temptation to infer that

the difference in size means simply a difference in the nutritive capacity, but further consideration shows this to be a hasty conclusion.

The important difference between the spores and gametes of *Ulothrix* is that the latter pair and fuse and the former do not. To obtain any suggestion as to the cause of this difference it is necessary to recall the conditions of spore-formation and gamete-formation. When the conditions favor maximum vegetative activity, neither spores nor gametes are produced. When the conditions are less favorable for vegetative activity, spores are produced; and when the plant is approaching the end of its activity, gametes are produced. It has been found possible to control experimentally the conditions that determine these various activities. The distribution of these functions in the ordinary life history of the plant is naturally related to its changing environment. The production of gametes in the simple plant we are considering is the last act in the life of the plant, an act induced by conditions that are bringing the activity of the plant to its close.

But why do gametes pair and fuse? It is obvious that more important differences than a difference in size have been developed in connection with the derivation of gametes from spores. The difference in size is visible, but in connection with it there develops a very different set of physiological conditions. This first stage of gamete production has been called "isogamy," but the name is only optically true. The same idea is expressed when such plants are said to be "unisexual." Exception may be taken to both of these terms. The gametes are alike in appearance, but that they are not alike in fact is evidenced by their pairing and mutual attraction. Morphological likeness may justify the term "isogamy," but for the term unisexual there is no excuse whatever. Sexuality, with its pairing sexual cells, implies two sexes, whether they can be distinguished or not. All sexual plants must be bisexual to be sexual at all.

The result of the sex act in these primitive sexual plants deserves attention. The zygote produced has the powers of an ordinary spore, in that it can produce a new individual, but the notable difference is that it does not germinate immediately. It is pro-

duced under conditions unfavorable to vegetative activity, and therefore unfavorable for the production of a new individual. The conditions that favor zygote-formation inhibit zygote-activity, and it responds with its heavy wall and dormant protoplast. Even when this zygote germinates, it may not produce a new individual, but the protoplast may divide at once to form spores. In other words, the protoplast of a zygote may function directly as a spore-forming protoplast. The inference is that the production of a vegetatively active individual or the production of spores depends upon the conditions for vegetative activity. If these conditions favor maximum vegetative activity, a vegetative individual will be produced; but if they do not favor maximum vegetative activity, spores will be produced. The succession of conditions at the opening of a growing season is just the reverse of the succession at the ending of a growing season. In the latter case there is a gradually waning activity, resulting in spore-formation following great vegetative activity; while at the opening of a season there is gradually increasing activity, the conditions first favoring spore-formation, and then vegetative activity.

The seasonal relation between spores and gametes lies at the basis of the changes which gradually established a definite alternation of generations. Spores are always as essential a feature of the life history as gametes, and in plants sexual reproduction is never the whole of reproduction.

A summary of the important facts in reference to the "origin of sex" may be stated as follows: (1) gametes have been derived from zoospores which have become so reduced by successive divisions as to be incapable of functioning as spores; (2) when first recognized by their behavior, gametes are alike in every visible feature, so that there is no evident distinction of sex; (3) a physiological differentiation of gametes is indicated by their mutual attraction in pairing, so that two sexes are present, although not distinguishable; (4) gametes are formed under conditions relatively unfavorable to either vegetative activity or spore-formation, representing the closing activity of a plant; (5) gametes therefore appear in response to unfavorable conditions that arise in the life history of a plant which is long enough to extend over a considerable

range of varying conditions; (6) the sex act results in a zygote which is formed under conditions unfavorable to vegetative activity, and therefore passes into a protected dormant condition; in other words, the conditions which favor the formation of a zygote inhibit its germination; (7) a zygote may function as an ordinary spore, producing a new individual, or it may produce spores, functioning like an ordinary protoplast; (8) the physiological changes involved by the introduction of the sex act are very great and far-reaching, for they include the mutual attraction of gametes, the organization into a single cell of the contributions of two cells, a provision for reducing the number of chromosomes which the sexual fusion has doubled, and the appearance of two kinds of individuals produced by spores and zygotes.

The differentiation of sex

The differentiation of sex usually discussed is morphological differentiation, which means in this case a visible difference in the size and activity of gametes, so that they can be recognized as male and female. The increase in bulk of one of the pairing gametes is observed to be due chiefly to the increased bulk of cytoplasm, and on this account the egg is said to have much greater nutritive capacity than its mate. This is probably not the only function of the cytoplasm of the egg in connection with the sex act, but whatever the functions may include, they are evidently as subsidiary to the act as are swimming appendages and mutually attractive substances.

Among the heterogamous plants, the variable gamete in appearance is the sperm, and its variability has to do chiefly with its swimming appendages, its form, and its amount of cytoplasm. From algae to gymnosperms, the apparatus for locomotion is developed in a variety of ways, reaching a high degree of specialization in such groups as the ferns and cycads. But among the angiosperms and higher gymnosperms a very different situation has developed, for motility has disappeared, even in its simplest expression. It follows that all the elaborate specialization of the sperm of ferns and cycads has to do with their motility, and not at all with their function as gametes. It is evident also that even the simple cilia

of the primitive gametes are no essential part of a sexual cell. The need for emphasizing this is apparent when it is realized that this secondary feature of a sperm has been regarded as its essential feature by those who demand rigid categories. When motile sperms were first discovered among gymnosperms, they were hailed as the only sperms in seed plants. In other words, the sperms of most seed plants were not regarded as sperms because they cannot swim.

Another rigid conception in reference to the sperms of angiosperms needs attention. Ciliated sperms are produced and discharged by the mother cell. This has led to so rigid a definition of a sperm that if the sperm generation is omitted it is concluded that there are no sperms. The usual formula for describing this situation has been to say that "the mother cell functions directly as a sperm," implying that in fact there is no sperm, but that the mother cell behaves like one. Since the test of a gamete through all its history is its behavior, it is difficult to understand such a statement, except that a secondary feature has been substituted for the essential one. It is obvious that if organization and discharge of a sperm by a mother cell are essential to secure freedom of approach to the egg, when another method of approach is secured, the necessity for discharge disappears. The protoplast within the mother cell and the discharged sperm are the same protoplast. The sperm mother cell of angiosperms behaves like a sperm because it is a sperm.

The obvious conclusion is that a sperm is a protoplast which fuses with another one to form a zygote; that in visible features it differs originally in no essential way from any other protoplast; that eventually it becomes less bulky than its mate on account of a difference in the amount of cytoplasm; that it often develops an elaborate swimming mechanism as a secondary feature; and that the swimming apparatus is eliminated when the necessity for swimming disappears.

The phenomenon of "double fertilization" in angiosperms introduces a situation that is suggestive. In this case a sperm fuses with another cell, so that there is the same mutual attraction as between egg and sperm, leading to contact and fusion, but there

is no production of a new individual. The inference is that the mutual attraction and fusion of two protoplasts is not all that is necessary for reproduction, and that mutual attraction is as much a secondary feature of sexual reproduction as is motility, and simply directs motility. There must be some fundamental difference between an ordinary cell, therefore, and one that has matured as an egg, but at the same time probably any protoplast may mature as an egg. It seems fairly well established that whatever of significance there may be in the sex act is found in the fusion of nuclei. When two protoplasts fuse, therefore, and do not produce a new individual, their nuclei must differ in some way from those of functioning sperms and eggs. One may imagine the adjustment of one nucleus to another before fusion can result in reproduction, and this mutual adjustment probably lies at the basis of sex-reproduction. It also probably explains the fact that sperms and eggs vary in their ability to fuse, and in the results of fusion.

Sexually differentiated individuals

The appearance of male and female individuals may be regarded as the extreme expression of sexual differentiation, which involves much more than the differentiation of male and female gametophytes, with their different sex organs. It is not necessary to present illustrations of the various situations this differentiation includes, for such a presentation would be merely a recital of life histories very familiar to morphologists. When the life histories of sexual plants are considered, ranging from the algae to the angiosperms, the following tentative conclusions are suggested:

Gametes are necessarily differentiated physiologically, and whatever explains this differentiation will explain the sexual differentiation of individuals. It seems to be a differentiation in chemical and physical constitution, which may or may not express itself in bodies visible in the sexual cells.

Whatever may be the cause of sexual differentiation, it is capable of being transmitted through generations of vegetative cells, until conditions favor its expression in the form of gametes and their associated structures. The implication of this statement is that sexuality does not arise *de novo* when gametes appear, but that

what may be called for convenience "sex-determiners" are always present in the plant body. These determiners are conceived of as representing substances that under appropriate conditions react in such a way as to determine the formation and character of the sexual cells.

Along with sex-determiners there must be sex-inhibitors, for it seems clear that every protoplast contains both determiners, but gamete-forming protoplasts produce only one kind of gamete. It seems probable, therefore, that every gamete-forming protoplast is equipped with two determiners and one inhibitor.

In the early history of sex the protoplasts of an individual differ as to this equipment, so that the individual is bisexual so far as gamete-formation is concerned. Later, all the protoplasts of an individual are alike in sexual equipment, and as a consequence individuals are sexually differentiated. Finally, with the appearance of heterospory, sexual individuals are permanently differentiated.

Apparently the amount of available nutrition holds no relation to the differentiation of sex, except as it inhibits the production of highly nutritive eggs by a body of small nutritive capacity, and at the same time permits the production of sperms. In other words, nutrition does not determine sex, but sometimes determines the opportunity for the expression of sex.

All the sporophytes contain both sex-determiners, and in sporogenesis they are transmitted to the spores, which may produce bisexual gametophytes or unisexual gametophytes, dependent upon the distribution of the inhibitors.

All fertilized eggs contain both sex-determiners and inhibitors, and may transmit them all to the sporophyte, in which case the sporophyte would produce spores functioning alike, or two kinds of spores differing in their inhibitors.

In the case of the monosporangiate sporophyte of seed plants, the fertilized egg transmits to the sporophyte only one inhibitor, which determines whether it produces megaspores or microspores.

The presence of sex-determiners and inhibitors determines not only the character of the gametes produced, but also the character of the sexual structures associated with them; and, in the case of

monosporangiate sporophytes, determines the development of a much wider range of structures than the appropriate sex organs.

Parthenogenesis

A strict application of the term parthenogenesis to the germination of an unfertilized egg is intended here. The facts that have accumulated in reference to parthenogenesis among plants seem to justify the following conclusions:

An egg may function as a spore in that it may germinate without fertilization. It seems evident, however, that an egg so differs from a spore in constitution that it needs a different kind of stimulus for germination. Usually this stimulus is applied in connection with the act of fertilization, but it may be applied in some other way.

The peculiar organization of the egg for fertilization is determined at the reduction division. If the reduction division does not occur, parthenogenesis is more likely to occur, and the egg is probably incapable of fertilization.

If spores are eliminated from the life history, as in animals and some plants, reduction occurs in connection with gamete-formation.

An egg necessarily produces a sporophyte, and a spore a gametophyte, but vegetative protoplasts of either generation may be organized to produce either generation; that is, they may function as eggs or spores, dependent upon the determiners they have received.

In general, therefore, parthenogenesis differs from reproduction by other protoplasts only in requiring a more specific stimulus, a fact which ordinarily prevents eggs from germinating unless fertilized.

Some conclusions concerning sexuality

Any general survey of the facts connected with sexual reproduction shows them to be very numerous and in some instances apparently contradictory, but they are all consistent with some general situation that determines sexuality. A review of the more prominent facts referred to in the preceding pages may sug-

gest a working hypothesis. There are three features belonging to the most primitive gametes that deserve attention: they are motile, small, and pairing cells.

It is evident that motility is not an essential feature of sexual cells, for early in the evolution of plants, one of the pairing gametes becomes passive, and finally both are non-motile. Motility, therefore, is a secondary feature common to both gametes at first, retained with remarkable persistence by the male gamete, but dispensed with entirely in most seed plants.

It is equally evident that the small size of the primitive gametes, as compared with the spores of the same plant, is not an essential feature of sexual cells. In other words, they are not gametes simply because they are smaller than the spores. Later in the history of plants, one of the pairing gametes becomes much larger than the spores, and still it is a gamete. The difference in size is due chiefly to the varying bulk of the cytoplasm, and in some seed plants the sperm is a naked nucleus. The conclusion is that the amount of cytoplasm is also a secondary feature of sexual cells. It is certainly true that the activity of the cytoplasm of the egg is intimately related to the act of fertilization, not only as a source of nutrition, but also as the source of an activating substance, which LILLIE has called "fertilizin," which determines the physiological moment of fertilization. It should be recognized, however, that even this activating substance is not an essential feature of sexuality, but belongs to the category of secondary features which aid in making the sex act possible.

The pairing of the primitive gametes is certainly a feature that belongs to all gametes, and yet there are pairing and fusing cells that are not gametes. If pairing and fusing are not peculiar to gametes, they do not represent the essential features of sexuality. Pairing seems to be a secondary feature, just as are motility and cytoplasm, and represents a mutual attraction that makes the sex act possible, just as motility is a mechanism that makes pairing possible.

It is certainly true, however, that the primitive gametes differ from the spores with which they are clearly associated in pairing and fusing, and this difference should be accounted for first. Since

spores are formed in conditions of greater vegetative activity than gametes, it is reasonable to suppose that the difference between spores and gametes is due to a difference in the activities of the protoplast in the two cases, a difference associated with declining vigor. Under such conditions, the products of metabolism will differ, and substances will be produced that do not appear when the protoplast is in full activity. This means that gametes will contain substances that spores do not, and among these substances are those that determine the mutual attraction that results in pairing. If this is true, it follows that different substances differentiate gametes into two kinds that are mutually attractive. These characteristic substances which appear later in the vegetative history of protoplasts may be regarded as among the products of waning metabolism. The appearance of different substances under such conditions is familiar in the case of the autumnal coloration of leaves.

It does not follow that these substances which characterize gametes appear only when the vegetative vigor of the plant as a whole is declining. This is generally true of such plants as the filamentous algae, but in more complex plants this decline of metabolic activity may occur in a region of the plant body, rather than in the body as a whole. For example, it is usually stated that the developing sex organs of mosses check the growth of the axis. It is a fair question to ask whether the sex organs do not appear because for some other reason growth has been checked. A checked growth indicates declining vegetative vigor, and this favors gamete-formation. Another illustration of the same fact may be obtained from the appearance of the sex organs of ferns. When a fern spore germinates, metabolism begins in a relatively feeble way, and during this early period antheridia are formed. Later, when the development of the gametophyte becomes more vigorous, sperm-formation may cease. The so-called "inhibitor" of sperms in this case, therefore, is the disappearance of the characteristic substances that belong to gametes, on account of the increasing vegetative activity of the protoplasts. In this case only such gametes can be formed as are characterized by a small amount of cytoplasm. Later in the history of the fern gametophyte, after

it has developed a well nourished body, cells in the apical region become checked in vegetative activity, the substances characteristic of gametes appear again, and eggs are produced.

We still face the fact that there are cell fusions, even pairing and fusing cells, which show the presence of the mutually attractive substances characteristic of gametes, but which do not represent the sex act. All such cases may be explained as evidences of declining vigor of the protoplast concerned, but if pairing and fusing are not peculiar to gametes, although universally displayed by them, what is the essential feature of gametes, or, in other words, of the sex act? The only answer that can be made is that gametes are pairing cells whose fusion results in the production of a new individual. This means that in addition to possessing mutually attractive substances formed in connection with declining metabolism, gametes possess nuclei so constructed that when the two fuse, a new individual is produced. This does not mean that neither gamete can produce a new individual alone, for parthenogenesis would contradict this. It means ordinarily that a new individual can be produced only after the nuclei have fused. In other words, the essential feature of sexuality must lie in the peculiar structure of the nuclei of the sexual cells. Whether this peculiar structure is chemical or physical, or both, must be a matter of opinion based on no direct evidence. Nor can it be true that gametes are peculiar in containing the factors of heredity, for these must have been handed down through all the cell generations leading to the gametes. Gametes furnish the opportunity for heredity to express itself, but so do spores, and so does vegetative multiplication.

If gametes are peculiar in the construction of their nuclei, how do they develop this peculiarity? The available evidence seems to make it clear that this gametic peculiarity, whatever it may be, is developed in connection with the reduction division. Among plants this division occurs generally in connection with spore-formation, and when there are no spores, as in *Fucus*, it occurs in connection with gamete-formation. In case the reduction division fails in connection with spore-formation, it has been observed that the resulting $2x$ egg is unable to fuse with the sperm. In any event,

the reduction division determines the sexual condition, and the peculiarity of this division, as compared with ordinary division, is related to the peculiar constitution of the nuclei of gametes as compared with other nuclei. If gametes have any structural peculiarity, it must be developed in connection with this peculiar nuclear division.

In well balanced alternation of generations, as in bryophytes and pteridophytes, there are many cell generations between spores and gametes and how the peculiarities of the gametes are transmitted through the cell generations of the gametophyte is a subject of speculation, but certainly something maintains a continuity between spores and gametes. In heterosporous plants, chiefly the seed plants, the cell generations between spore and gamete become fewer and fewer, until finally sperms are reached in two successive cell divisions, and the eggs are reached in one to three successive divisions. The next advance would be the elimination of spores entirely and the occurrence of reduction in connection with gamete-formation, as in animals.

In conclusion, the impression one obtains of sexuality as a method of reproduction is that it represents protoplasts engaged in reproduction under peculiar difficulties, that do not obtain in reproduction by spores or by vegetative multiplication, and that its significance lies in the fact that it makes organic evolution more rapid and far more varied.

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